

Helminth Parasites of Bowfin (*Amia calva*) from South Carolina

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ABSTRACT: Twelve bowfin (*Amia calva*) collected from 3 backwaters off the Savannah River in South Carolina were examined for helminth parasites. Thirteen species were found: 5 trematodes, 2 cestodes, 5 nematodes, and 1 acanthocephalan. Five species (2 trematodes, 2 cestodes, and 1 acanthocephalan) occur regularly and are considered core species. Species richness and community abundance were high compared to published studies on other species of freshwater fish. Although mean number of species and diversity were comparable to infracommunity patterns observed for many aquatic birds, the abundance of helminths was reduced. Host specificity and broad feeding preferences are suggested as important determinants of helminth community structure in bowfin.

KEY WORDS: bowfin, *Amia calva*, helminths, frequency, intensity, species richness, infracommunity composition.

Bowfin, *Amia calva* L., are the only extant species of the Amiidae. They are found throughout most of eastern North America in a diversity of freshwater habitats. Their large size and abundance makes them conspicuous components of the fish assemblage in swampy, vegetated bays of lakes and rivers (Scott and Crossman, 1973; Pfieger, 1975).

Compared to many North American freshwater fishes, comparatively little information is available on the natural history of *A. calva* (Reighard, 1904; Holland, 1964; Cartier and Magnin, 1967; Stacy et al., 1970). This also characterizes information on their helminth parasites with most studies providing either descriptions of new taxa or reports of species occurrences (e.g., Sogandares-Bernal, 1955; Sillman, 1962; Premvati, 1969). Several surveys indicate compositional variability between locations (Van Cleave and Mueller, 1934; Bangham and Hunter, 1939; Bangham, 1941; Bangham and Venard, 1942; Bangham, 1955; Robinson and Jahn, 1980); none provides analysis and few present data potentially useful to understanding the organization of parasite communities. Recent comparative treatments of helminth infracommunity structure have suggested that those in freshwater fish are species-poor (Kennedy et al., 1986). In the present study, we show that bowfin can have parasite communities that are surprisingly rich for freshwater fish, with high proportions of frequently co-occurring species.

Materials and Methods

Bowfin were collected during the second week of July 1988 by electrofishing 3 backwater locations off the Savannah River between river miles 136 and 158 in Aiken and Barnwell counties, South Carolina. Individuals were returned live to the laboratory where they were measured (total length) and sexed (6 male, 6 female) before necropsy. Age was determined from the gular plate (Holland, 1964). Alimentary tracts were immediately removed and quickly frozen in a dry ice-95% ethanol mixture as described by Bush and Holmes (1986). The remaining viscera and carcass were then individually frozen for later examination. Esophagus, stomach, and intestine were separated, measured, and then examined. All worms were counted and identified using either temporary wet mounts or specimens that were fixed and prepared as permanent mounts. Voucher specimens have been deposited in the United States National Museum Helminthological Collection (USNMH 81477-81483) and the University of Nebraska Parasitology Collection (HWML 31614-31621). Noncatalogued species (unidentified Spiruridae, *Capillaria* sp., *Thynascaris brachyurum*) were either uncommon or damaged, but specimens have been retained by 1 of the authors (J.M.A.).

Terminology follows definitions established by Margolis et al. (1982). Frequency of infection (*N*) is the number of infected hosts. Predictability of infracommunity composition was measured using Jaccard's coefficient (qualitative, based on species presence/absence) and percent similarity (quantitative, based on numerical proportions of each species). Brillouin's index, appropriate for fully censused communities (Pielou, 1975), provided a measure of infracommunity diversity. Values were calculated using common logarithms; for comparison with data of Kennedy et al. (1986), where Brillouin's index was calculated using natural logarithms, values can be multiplied by 2.303. Fisher exact tests (with an adjusted $P = 0.005$ to maintain an "experiment-wise" error rate of $P \leq 0.05$) were calculated for the common helminth species to test for differences in frequency of infection and host sex; differences in intensity of infection were examined using

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the Mann-Whitney *U*-test. Correlations between infection parameters and host factors were tested using Spearman rank correlation (r_s). Rejection of the null hypothesis was at $P \leq 0.05$. Values are expressed as mean \pm 1 SE.

Results

Twelve adult bowfin were examined for helminths. Fish ranged in size from 520 to 680 mm (589 \pm 16 mm) and were 4–8 years old. The presence of recrudescing gonads indicated all individuals were sexually mature adults. The number of fish examined might be considered low relative to other studies on fish parasites but, based on cumulative species richness, >90% of the helminth species found were recovered from just 6 bowfin. Thus, the sample size should be sufficient to examine patterns of infracommunity structure.

Each bowfin was infected, and helminths were found only in the alimentary tract (Table 1). Individual fish harbored between 5 and 8 species of helminths and 18–269 individuals; mean species richness was 6.5 \pm 0.3 and community abundance averaged 114 \pm 27 individuals. Brillouin's index ranged from 0.32 to 0.80, with a mean value of 0.52 \pm 0.04. The intestinal helminth assemblage had the greatest number of species with 3 to 6 species (4.8 \pm 0.3) per fish. Number of worms found in the intestine ranged from 7 to 230 individuals (63 \pm 22). Community diversity of the intestinal helminth assemblage varied from 0.15 to 0.43 (0.30 \pm 0.02). Mature or gravid individuals of all species were represented except for *Thynascaris brachyurum*. Frequency, prevalence, mean intensity, and site of infection are presented in Table 1.

Composition of the helminth assemblage was numerically dominated (>95% of individual worms) by trematodes (5 species) and cestodes (2 species). Two species of trematode, *Macroderoides typicus* and *M. trilobatus*, and the cestode, *Proteocephalus perplexus*, were commonly found and accounted for 85% of all individuals. *Azygia angusticauda*, *A. longa*, *Haplobothrium globuliforme*, and *Neoechinorhynchus cylindratus* also occurred frequently, but in moderate to low abundance. The remaining species, including the 5 nematode species, were infrequent and abundance was low.

There were no differences in the frequency or mean intensity of infection between host sexes for any helminth species. There were also no significant correlations between either the num-

ber of individuals of each species or the total number of helminth individuals and either host size or length of the intestine. These patterns suggest that the number of worms is not a function of the size of the host environment.

Qualitative faunal similarity among hosts was quite high (Jaccards coefficient = 60.0 \pm 1.9%). Quantitative similarity was comparatively lower (percent similarity = 45.3 \pm 2.8%) indicating some disparity in the abundance of species across infracommunities. Frequency of occurrence and infracommunity abundance were significantly correlated ($r_s = 0.67$, $P < 0.05$). The co-occurrence of *M. typicus* and *P. perplexus* in 11 hosts, which were often the 2 most abundant helminths, influenced this correlation. In pairwise comparisons between the intensities of all species pairs (using only species where $N \geq 4$), only *P. perplexus* and *M. typicus* had a significant association ($r_s = 0.67$, $P < 0.03$); there was an equivocal positive association between *Haplo-nema immutatum* and *N. cylindratus* ($r_s = 0.95$, $P = 0.05$). Frequency distribution of the prevalences of the helminth species distinguished 3 groups of species. Parasites whose prevalence was >80% were regarded as core species, and included *P. perplexus*, *H. globuliforme*, *A. angusticauda*, *N. cylindratus*, and *M. typicus*. Species with prevalence <20% are regarded as satellite species, and those intermediate in prevalence are regarded as secondary species (as in Bush and Holmes, 1986).

Discussion

The helminth fauna of bowfin from this area of the Savannah River is a representative subset of the species found in other parts of its geographical range (Van Cleave and Mueller, 1934; Bangham and Hunter, 1939; Bangham, 1941; Bangham and Venard, 1942; Bangham, 1955; Robinson and Jahn, 1980). With the exception of *Capillaria* sp., every species has previously been reported from bowfin. *Macroderoides trilobatus* had only been reported before from bowfin collected in the Ochlocknee River, Georgia (Taylor, 1978). In this study, it is the absence of monogeneans or larval trematodes, cestodes, or nematodes that is most unique.

The high species richness and diversity of the helminth assemblage from bowfin in this locality are unusual among freshwater fish. Most studies indicate helminth communities of a variety of freshwater fish are species-poor with low or variable abundance and low community diversity

Table 1. Frequency, prevalence, mean intensity, and site of infection for gastrointestinal helminths of bowfin (*Amia calva*).

Helminth species	Site*	N (%)†	Mean intensity (SE)
Trematoda			
<i>Azygia angusticauda</i> (Stafford, 1904) Manter, 1926	S, SI	12 (100)	6.8 (1.9)
<i>Azygia longa</i> (Leidy, 1851) Manter, 1926	S, SI	5 (42)	1.0 (0.0)
<i>Macroderoides typicus</i> (Winfield, 1929) Van Cleave and Mueller, 1932	LI	11 (92)	35.0 (13.2)
<i>Macroderoides trilobatus</i> Taylor, 1978	SI	6 (50)	44.7 (22.9)
<i>Microphallus opacus</i> (Ward, 1894) Ward, 1901	SI	2 (17)	8.5 (7.5)
Cestoda			
<i>Haplobothrium globuliforme</i> Cooper, 1914	SI	10 (83)	2.0 (0.5)
<i>Proteocephalus perplexus</i> LaRue, 1911	S, SI	12 (100)	44.9 (14.2)
Nematoda			
<i>Camallanus oxycephalus</i> Ward and Magath, 1917	LI	4 (33)	2.5 (1.5)
<i>Capillaria</i> sp.	E	1 (8)	1
<i>Haplonema immutatum</i> Ward and Magath, 1917	SI	4 (33)	3.0 (0.8)
Unidentified Spiruridae	SI	2 (17)	1.0 (0.0)
<i>Thynascaris brachyurum</i> (Ward and Magath, 1917 sensu Van Cleave and Mueller, 1934)	S	1 (8)	1
Acanthocephala			
<i>Neoechinorhynchus cylindratus</i> (Van Cleave, 1913) Van Cleave, 1919	SI	10 (83)	3.4 (0.8)

* E = esophagus; S = stomach; SI = small intestine; LI = large intestine.

† N (%) = frequency, number of fish infected (prevalence, % of fish infected).

(Kennedy et al., 1986). Excluding this study, infracommunity richness for bowfin ranges from 2 to 4 species per location (Bangham and Hunter, 1939; Bangham, 1941; Bangham and Venard, 1942; Bangham, 1955), whereas most freshwater fish typically have fewer than 2 species per host individual (Kennedy et al., 1986). Patterns of species richness and diversity observed here for bowfin are comparable to helminth communities in many aquatic birds (Kennedy et al., 1986; Stock and Holmes, 1987; Holmes, 1990). Fundamental differences in helminth infracommunity structure between ectotherms and endotherms is suggested to be a function of physiological and behavioral processes affecting the acquisition of parasites by individual hosts. The energy demands of endothermy increase exposure to infected intermediate hosts, and contribute to the development of larger, more complex communities (Kennedy et al., 1986). Factors contributing to differences among fish species, and apparent parallels in community complexity with some aquatic birds are, however, still unclear.

Host specificity makes an important contribution to the helminth community structure for bowfin from this locality. Unlike the pattern of

low helminth assemblage similarity within and between locations for many species of freshwater fish (Esch et al., 1988; Kennedy 1990), the presence of a central block of frequent, regularly co-occurring core species results in considerable qualitative similarity among bowfin infracommunities. Based on patterns from the literature (see Hoffman, 1967; Margolis and Arthur, 1979 for summary checklists), 3 core species (*P. perplexus*, *H. globuliforme*, and *M. typicus*) are host specialists of *Amia* as are the 2 secondary species, *H. immutatum* and *M. trilobatus*. The remaining 2 core species (*N. cylindratus* and *A. angusticauda*), as well as all satellite species, are host generalists reported from a wide variety of freshwater fish.

Qualitative similarity for 6 surveys (Van Cleave and Mueller, 1934; Bangham and Hunter, 1939; Bangham, 1941; Bangham and Venard, 1942; Bangham, 1955; Robinson and Jahn, 1980) is low ($30.1 \pm 4.3\%$) suggesting considerable variability in the helminth assemblage among different bowfin populations. Compositional differences between populations are predominantly due to species replacements of host generalists; specialist species only account for ca. 25% of the helminth species reported from bowfin. This pat-

tern, therefore, suggests that processes determining the abundance of host generalists (e.g., availability of suitable intermediate hosts, geographic location, or composition of the host community) strongly influence the richness and diversity of the helminth assemblage. This view is contrary to suggestions by Toft (1986) that species richness in parasite communities should be enhanced by a high degree of host specificity.

A second factor that contributes to helminth community structure appears to be host feeding preferences. Examination of food habits of adult bowfin suggests that they are omnivorous, but forage extensively on a variety of fish and crustaceans such as grass shrimp and crayfish (Holland, 1964; Cartier and Magnin, 1967; Stacy et al., 1970). The proportions of parasites derived from different intermediate hosts support these patterns, and emphasize the importance of fish and crustaceans to helminth acquisition. Illustrated by the present study, helminths using fish intermediate hosts represent approximately 50% of the species and 80% of the community abundance while those using crustaceans account for 20–30% of the species. Life cycles for the remaining species are either direct (15% of the species) or are incompletely known (*H. immutatum*, *Capillaria*, unidentified Spiruridae).

Kennedy et al. (1986) suggest that broad diets should promote development of diverse helminth communities and that selective feeding can lead to large infrapopulations. Price and Clancy (1983) provide evidence that predaceous fishes have richer helminth communities than fishes lower in the food chain. The feeding preferences of bowfin are consistent with these predictions for the establishment of diverse communities and large infrapopulations ("large" relative to most other ectotherms). These features suggest the existence of predictable, strong trophic linkages among bowfin that encourage qualitative consistency in infracommunity composition within a location. Although other freshwater fish are opportunistic, generalist omnivores, depauperate helminth infracommunities in these species may reflect either greater temporal and spatial variation in patterns of prey utilization or intermediate hosts that do not have high prevalence or intensity of infection. Similar observations for the development of depauperate infracommunities in other ectotherms have been made by Goater et al. (1987) and Aho (1990).

The high helminth infracommunity richness and diversity of bowfin from this location, com-

pared to other studies on bowfin, are thought to be habitat related. Where information on collection site is provided, the helminth fauna of bowfin has been predominantly studied in lentic environments. Bowfin examined in this study were found within the vicinity of protected, vegetated backwaters off the main river channel. These are highly productive habitats compared to main channel reaches (Brinson et al., 1981); presence of woody debris and submerged aquatic vegetation associated with these areas serve as valuable cover for a diversity of fish species and substrate for invertebrate production. The preference of bowfin for low velocity, clear water habitats (Scott and Crossman, 1973; Pflieger, 1975) leads to high spatial and temporal overlap of host and parasite life histories. This can enhance helminth transmission and circulation dynamics. While their somewhat isolated nature makes them analogous to small lakes, these backwaters are also continually exposed to immigration by invertebrates and vertebrates dispersing helminth larval stages. As a result, helminth species present in a habitat may be reintroduced frequently (as in the rescue phenomenon of island biogeography; Schoener, 1983) or colonized by new helminth species. The dynamic processes operating within these backwaters provide, and maintain, conditions promoting development of complex local helminth communities. As a consequence of these processes, bowfin helminth infracommunity structure approaches helminth species richness and diversity features found in several species of aquatic birds. We would also expect other fish found in these environments to have richer, and more predictable helminth infracommunities than typically found in lentic habitats.

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